

PROCEEDINGS
OF THE
BIOLOGICAL SOCIETY OF WASHINGTON

REVISION OF THE MILLIPED GENUS *WAMOKIA*
CHAMBERLIN FROM THE SIERRA NEVADA OF
CENTRAL CALIFORNIA (DIPLOPODA:
POLYDESMIDA: XYSTODESMIDAE)

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The genus *Wamokia* Chamberlin consists of a moderately sized group of milliped species occupying a small region of the central Sierran Foothills of California. They may be recognized by the dull yellow ground color with a dark mid-dorsal stripe and orange paranota.

Unlike most groups of western diplopods, *Wamokia* has been almost totally neglected by students of the Diplopoda. Described by R. V. Chamberlin in 1941, the original diagnosis distinguished the genus adequately, but left some doubt about the identity of *placera* Chamberlin, the type species. An illustration given of the gonopod from the ventral aspect is of assistance for identification, but does not show enough of the important femoral endite. However, a sketch of the type prepared by Richard L. Hoffman and loaned to us has been of great value in fixing the identity of *placera*. Chamberlin and Hoffman (1958) misspelled the genus as *Waimokia* in their checklist and cited the type locality as occurring in Tulare County, though it is actually in El Dorado County. Buckett (1964) corrected the latter error although he, too, misspelled the generic name.

This work was initiated through an agreement with Dr. Hoffman, who had discovered two undescribed species of *Wamokia* in some xystodesmid material we loaned him for his revisionary work. Subsequently, further field work was

carried out which revealed the existence of four other undescribed species thus making a total of seven entities in the genus.

Under the variation section of each species, measurements are given to help characterize populations. Whenever enough material existed, five males and five females chosen at random were used to compute the values. For the "average population length" the total of the 10 specimens was used. For length/width ratios, full width, including paranota, was used.

ECOLOGY

The genus *Wamokia* is composed of a group of species which range from elevations of 500' on the Cosumnes River to 3200' at Foresthill, Placer County. Yet the entire known range of the genus does not exceed 50 miles in the greatest dimension.

A number of aspects of the habitat are shared by all the species in the genus. *Wamokia* are almost always associated with the bright ochre Aiken Clay (see Storie, 1927) soil which dominates the Sierran Foothills of El Dorado, Placer and Nevada Counties, specimens being found actually within the soil or in the zone between soil and litter. It is quite possible that the geographic boundaries of the genus are influenced by the distribution of this soil type. A common denominator of all collections is the occurrence of *Quercus* spp., usually *wislizenii* A.DC. and *kelloggii* Newb. in the immediate vicinity of the collecting spot. The immediate habitat of *Wamokia* populations appears to be influenced strongly by vegetation in connection with the soil type.

In general, *Wamokia* species occur in large populations and are easily collected. Often these populations occur in relatively restricted areas on slopes and are probably exploiting an optimum habitat not immediately evident to the observer.

Ecological relationships with other species: Most Californian xystodesmid species occupy mutually exclusive geographic regions, probably a result of competition for the same niche; such is the case with species of *Wamokia*. Immediately south of the Cosumnes River, the distribution of *Wamokia* ceases

and *Amplocheir* Chamberlin becomes abundant and continues south through Madera County. Like *Wamokia*, *Amplocheir* species inhabit areas of clayey soil and shallow leaf litter, yet the soil and vegetation are qualitatively different than in areas inhabited by *Wamokia*. The closest northern neighbor of *Wamokia* appears to be *Hybaphe* Cook, which occurs in Tehama and Shasta Counties in California.

Only two other genera of xystodesmids are known to occur sympatrically with *Wamokia*. *Sigmocheir* Chamberlin which occurs throughout the central and southern Sierras, was collected on the same hillside with *W. hoffmani* new species, at the Cosumnes River southeast of Latrobe. Also, an undescribed species of *Hybaphe*, to be described elsewhere, occurs in the American River Canyon near Auburn. Near the bottom of the south wall of the canyon, where vegetation is luxuriant and the soil rich, the *Hybaphe* species is found. Higher on the wall, where the slope is steeper, soil leached, and litter thin, one finds many *W. discordis* new species, and very few *Hybaphe*. Presumably, competition with *Hybaphe* and *Sigmocheir* is avoided in these cases by different preferential habitats.

TAXONOMIC CHARACTERS

Gonopods: As in most groups of millipeds, the gonopods exhibit obvious interspecific differences. As with any structure which is so genetically pliable, however, considerable variation occurs intraspecifically.

The telopodite branches about one-third its length from the hinged connection to the coxa into two structures, a long, narrow tibiotarsus carrying the seminal canal, and a femoral endite of varying shapes and sizes, usually with a mesally curving distal process and a smaller lateral process.

The tibiotarsus is simplest, hence offering fewer diagnostic characters. On the lateral margin distad of the femoral process is a spine in some species. In specimens of *discordis* or *sierrae* new species, the spine may be present or absent. In species which constantly possess it, variation is expressed in relative size of the spine, whether it is simple or bifid, and even its position on the tibiotarsus.

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The distal portion of the tibiotarsus curves strongly mesad in all species except *remota* new species, the nature of this curvature being characteristic of the species.

The femoral endite possesses a serrate ventrobasal margin in *remota* and *dentata* new species, the other species all having smooth margins in the specimens examined. The body of the prefemoral endite basically possesses two processes, a distal process curving mesad, and a small lateral process. One species, *hoffmani*, possesses a basal process as well, which projects mesad. The terminology used for these structures was constructed only for convenience, so homologies are not necessarily presumed between related groups for all structures bearing the same terms.

Variation in the femoral endite is trenchant, the size, shape and curvature of the distal process being generally constant within species, the only exception being *discordis*, in which the apex may be acute or rounded. The lateral process is useful only with regard to general size. Although well developed in most specimens of *remota*, in one specimen the lateral process is represented only by a rounded bump. In *discordis* it may be simple or bifid, and the length may vary up to 50 percent.

Cyphopods: The mesoproximal aspect of the cyphopods displays amazing differences between some species, although the usefulness of these structures is partly canceled by the strong variability present. Nonetheless, most female specimens can be identified by the cyphopods.

Sexual dimorphism: During our field work with *Wamokia*, we were soon able to easily distinguish male from female specimens from a considerable distance, the following characteristics making this possible. Female length/width ratios are lower than in males. Accentuating this disparity, each paranotum of females projects out less than 25 percent the width of the body cylinder, whereas in males the paranota approach 40 percent of the cylinder width. Also, females possess very thin legs, whereas in males, the legs are quite robust. Females are also slightly longer than males on the average.

Genus *Wamokia* Chamberlin

Wamokia Chamberlin, 1941. Bull. Univ. Utah, Biol. ser. 6(5):14.

Waimokia Chamberlin and Hoffman, 1958, *Lapsus calami*. Bull. U. S. Nat. Mus. No. 212:53; Buckett, 1964, *Lapsus calami*, Ann. list Diplopoda California, p. 10.

Type species: *Wamokia placera* Chamberlin, by original designation.

Diagnosis: *Wamokia* may be recognized by the small size (19–32 mm), thin exoskeleton with orange-brown coloration and with orange, acute paranota; second and third legs of male with coxal processes present and sternal processes lacking; male gonopods with coxae joined firmly together, telopodite with long, simple tibiotarsus and simple or complex prefemoral process.

In order to facilitate future comparison of xystodesmid genera, a thorough description of the genus is presented below.

Description: Color in life usually beige on prozonites, medium grey on metazonites and bright orange on both surfaces of lateral and posterior margins of paranota; sometimes orange color extends across metazonite; telson orange dorsally; a dark dorsomedial longitudinal line present.

Head oval, with coronal suture smooth, prominent, dividing between antennae into two frontal sutures which are evident only for distance between antennae; one pair of long supra-antennal setae present on each side of coronal sutures; frons with a pair of setae on each frontal suture, upper setae between antennae and lower seta just ventromesad of antennae; frons smooth, but with shallow transverse sculptured lines; lower part of frons with transverse row of setae; another row of setae lining lateral margin of facial shield; clypeus with transverse row of about twenty setae; labrum also with about twenty setae; genae smooth, with impressed groove parallel to supra-antennal groove; antennae widely separated, distance between them equal to length of second antennal segment; first antennal segment subcircular and broader than other segments, with two setae longer than segment; second segment long, proximally curving slightly dorsad, then curving slightly in opposite direction, with long distal setae; segments 3–5 subequal in size and shape, slightly shorter than segment 2, narrow proximad and wide distad; segment 6 subequal in length to segment 2, but narrower, more densely setose; segment 7 small, densely setose, truncate; four terminal sense cones set in concavity of apex.

Body subcylindrical, paranota moderately developed, projecting out from body on each side 20 percent to 40 percent width of cylinder, projecting downward at about thirty degrees from horizontal at just above mid-body height, posterior margin higher than anterior margin; dorsa of tergites smooth; prozonites separated from metazonites by shallow groove dorsally, this groove disappearing below paranotal margins; repugnatorial pores round, opening laterally on paranota near posterior margin; pleural areas smooth, coriaceous; anterior tracheal

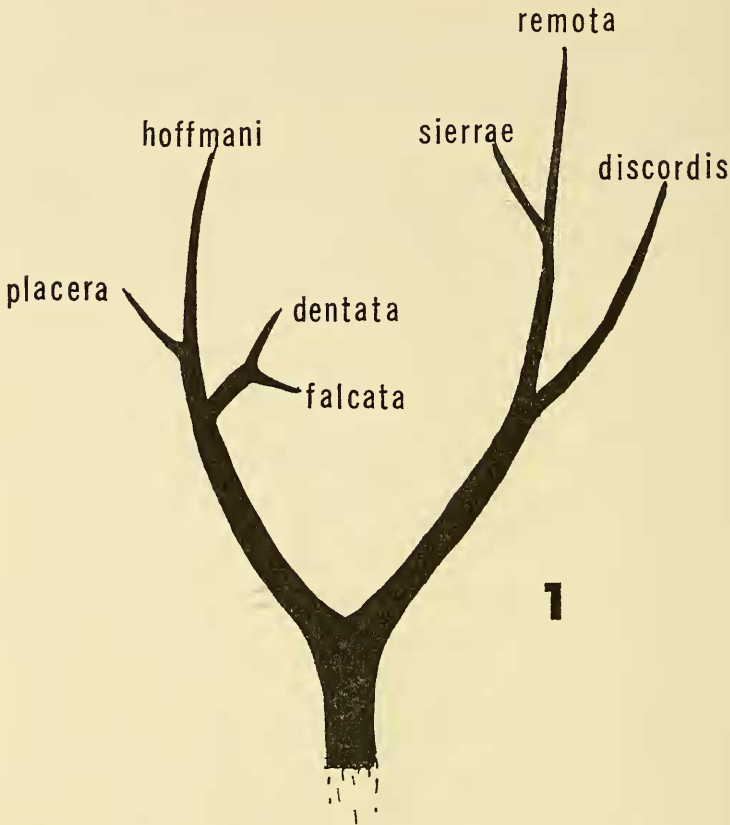


FIG. 1. Dendrogram showing relationships within species of *Wamokia*.

aperture oval, vertically elongate; posterior aperture oval, less elongate. Sterna smooth, raised out slightly from level of body mesially, but much laterally, the coxae projecting forty-five degrees down from horizontal; sterna not produced up on legs, a transverse groove present on sternum between legpairs on each segment.

Collum wider than head but narrower than following segments, with anterior margin curving in even semicircular arc, the posterior corners even with posterior margin of segment; collum not much arched, not reaching ventrad to paranotal margin of second tergite; segments 3-8 with antero-lateral corners increasingly rounded, posterolateral corners increasingly produced; near posterior end of body much of lateral margins of paranota nearly straight; segments 17 and 18 progressively smaller and narrower, segment 19 much reduced, paranota often not



FIG. 2. Distribution map of species of *Wamokia*.

projecting caudad beyond posterior corners of segment 18; telson sub-triangular, broader than long, with two pairs of dorsal setae, one pair of setae on lateral margin cephalad, one pair laterad of posterodorsal setae, and two pairs of apical setae; anal valves smooth, distinctly surpassed by mucro, with two pairs of setae lining lips; preanal scale

large, sub-lenticular, about half as long as broad, with a pair of setae on posterior margin; tergum of twentieth segment visibly ringing entire segment anteriorly.

Legs long, femur exceeding lateral margin of paranota; male with leg segments much broader and more robust than female; legs with coxa cylindrical, slightly longer than broad; prefemur subequal in length to coxa, lateral margin bulging; femur the longest segment, very narrow basally and widening apically; postfemur the shortest segment and narrower than previous segments; tibia equal in length to postfemur, but narrower; tarsus narrowest segment, and about as long as prefemur; tarsal claw large and curved mesially, legs generally sparsely setose, the tarsus more densely setose, and prefemur possessing a long seta based just proximad of distal spine; distal subtriangular prefemoral spine beginning on segment 9 and progressively increasing in size posteriorly, the posterior leg of each segment with slightly greater spine development; second coxae of male each with a short, subcylindrical ventral process; third coxae with larger pair of cylindrical processes produced anteroventrad; legs 1 and 2 with coxae adjacent, projecting ventrad; legs 3-7 with coxae increasingly separated; legs 8-28 with coxae separated by about two coxal widths, the posterior legpair of each segment separated slightly more than anterior legpair.

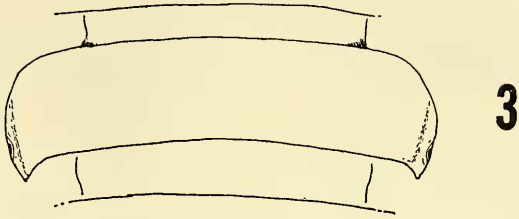
Gonopod socket large, oval, extended cephalad three-fourths width of prozonite and caudad to within two-thirds coxal width of posterior margin of segment.

Gonopods large, wholly filling socket, with telopodite and much of coxa extruding from body cavity, the telopodite joined to coxa at ninety degrees and produced cephalad, projecting between seventh legs; coxae very large, broad, with a short coxal apodeme produced proximad from mesal margin of coxa; telopodite rigid, but fixed to coxa at a flexible joint.

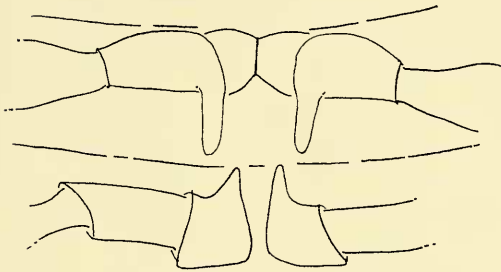
Coxae of gonopods joined together by transverse muscle tissue as well as the sclerotized sternal connective where coxae meet distally. Telopodite with femoral endite of varying shapes emerging from the femoral region and situated cephalad of tibiotarsus; tibiotarsus long and thin for most of its length, often apically curving mesad and sometimes again distad, and sometimes with a lateral spine located about mid-length; femoral endite composed of main body from which project two or three processes, a *distal process* which projects mesodistad, a *basal process* which projects mesad and a small *lateral process* which projects laterad; solenite emerging from coxa distally on anterior face mesad of telopodite base, immediately arching up to telopodite away from body of gonopod, proceeding distad in seminal canal mesad of femoral endite, thence along center of tibiotarsus to apex.

GENERIC RELATIONSHIPS

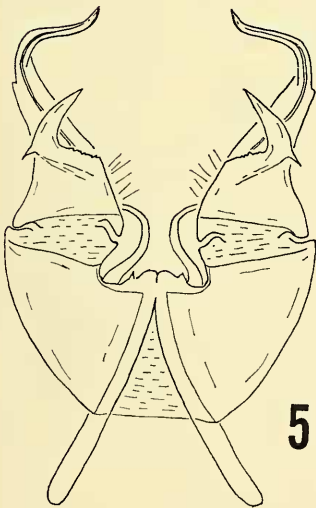
Characters of *Wamokia* appearing most significant at the generic level are the following: gonopods with coxae large and rigidly joined together



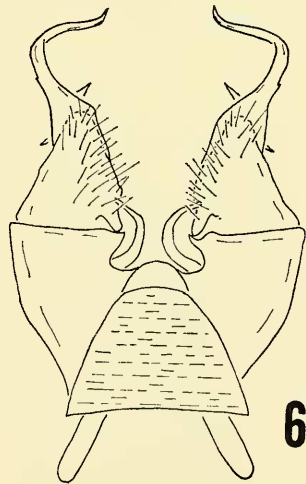
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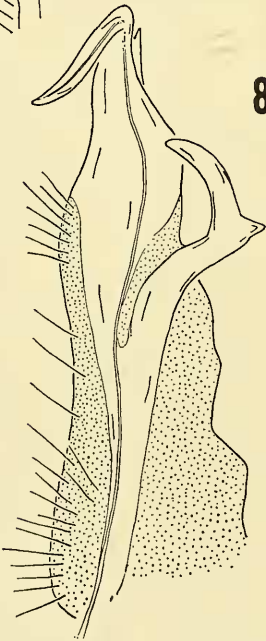
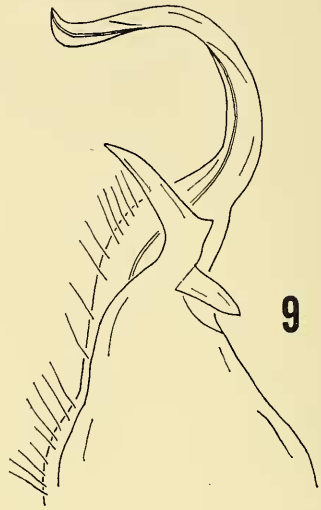
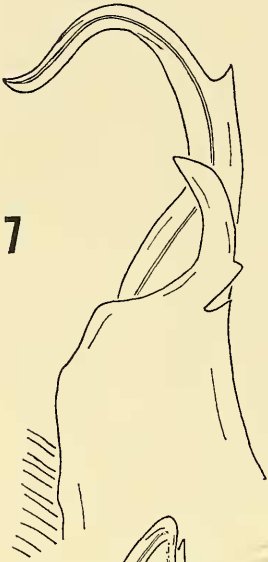


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FIGS. 3-6. 3. *W. placera*, male. Dorsal aspect of tenth tergite. 4. *W. placera*, bases of second and third legs. 5. *W. dentata*, paratype male. Gonopods in vertical position. 6. *W. dentata*, paratype male. Gonopods, posterior aspect.



with a sternal structure; telopodite movably hinged to coxa and bent at right angle; second and third legs of male with rounded coxal projections; second legs of female with cylindrical processes on coxae; dorsum smooth, with cuticle thin and paranota with acute posterolateral corners; color yellow-brown with orangetipped paranota.

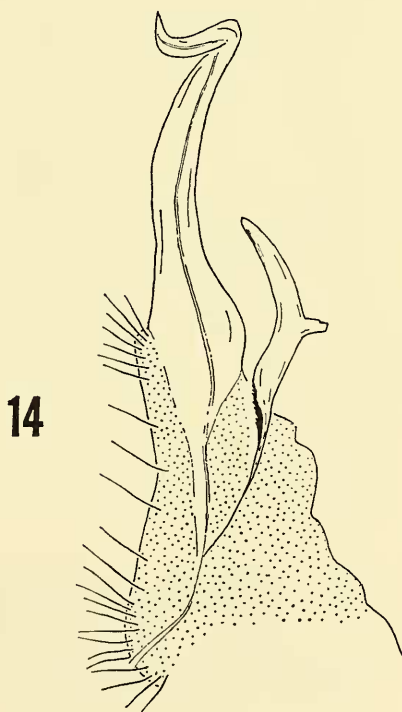
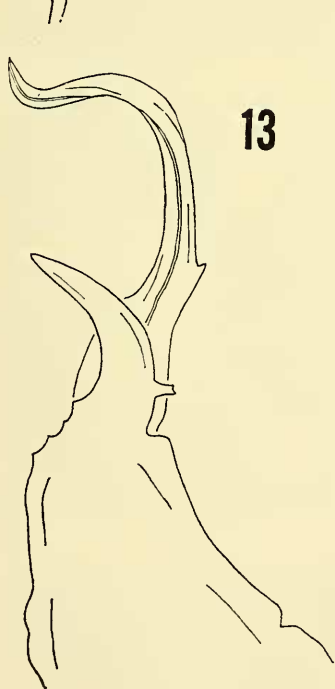
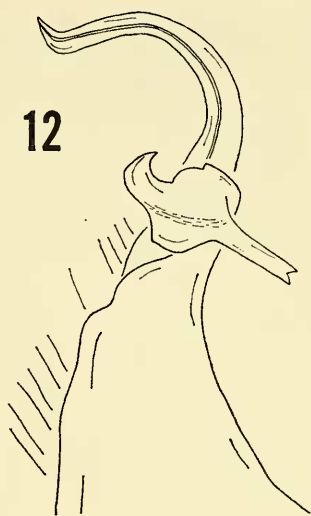
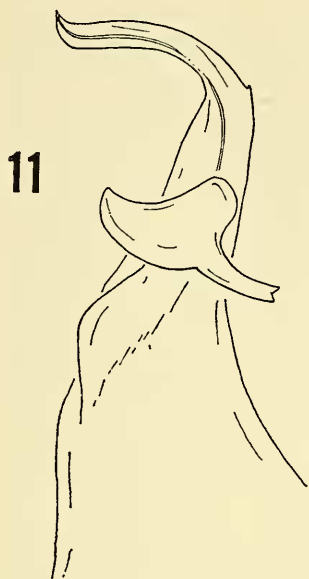
On the basis of the characters given above, *Wamokia* appears to be closely related to *Amplocheir*, an inhabitant of the more southerly Sierra Nevada of California. Differing only in the configuration of the gonopod telopodite and presence of dorsal tubercles, *Amplocheir* can be easily mistaken for *Wamokia* in the field. That the genera should be maintained with separate status is a belief based primarily on the discontinuity in the gonopods, which is considerable. A third genus in this group is *Paimokia* Chamberlin (sensu stricto). Sharing most characters with *Wamokia* and *Amplocheir*, *Paimokia* differs in having the dorsum well-tubercled, and the paranota rounded rather than angular. *Motyxia* Chamberlin and the *Xystocheir* group (*Cheirauxus* Chamberlin, *Delocheir* Chamberlin) appear to be more remotely related to *Wamokia*, with *Motyxia pior* Chamberlin possessing sternal processes on the fourth legs, no coxal processes on the third legs, rounded paranota and a differently shaped gonopod aperture, with gonopod coxae joined near their bases. *Xystocheir acuta* Cook from Palo Alto, California, possesses sternal processes on third and fourth legs, a larger, much more robust body with much thicker cuticle, tuberculate dorsum and a differently shaped gonopod aperture.

SPECIES RELATIONSHIPS

The species of *Wamokia* may be broken into two general groups, which differ by the presence or absence of a torsion in the femoral endite of the male gonopods. The four southern species, *dentata*, *falcata*, *hoffmani*, and *placera* lack the torsion and form a rather close group, although *hoffmani* possesses the unusual basal process. Further to the north, the species *discordis*, *sierrae* and *remota* form a group in which the femoral endite is twisted at the base so that the distal process curves oppositely from that of the other species group. Setting the small, simple femoral process as the primitive condition, *falcata* would be the least modified species and *discordis* or *remota* the most modified. A dendrogram expressing these ideas is presented (see fig. 1).

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FIGS. 7-10. (Right male gonopods). 7. *W. falcata*, paratype; anterior aspect. 8. *W. falcata*, paratype; mesal aspect. 9. *W. placera*; anterior aspect. Collected 3 miles southwest of Placerville, El Dorado County. 10. *W. placera*, holotype male; mesal aspect. Collected from Placerville, El Dorado County.



of frons with irregular transverse row of 8 setae; clypeus with irregular row of 22 setae; labrum with row of 30 setae; gular groove very shallow; a series of 6 setae present along lateral margin of facial shield between labrum and ventrodistal corner of antennal groove. Tergites smooth, with minute impressed longitudinal striae; collum with front margin evenly curving, caudolateral corners not surpassing posterior margin of segment; segment 19 narrower than anterior width of segment 18, with paranota of 19 projecting caudad only slightly beyond posterior margin of segment; telson subtriangular, with 14 setae normally placed. Pleural area smooth; sterna low medially, pronounced laterally, smooth except for minute impressed longitudinal striae, a distinct transverse groove present between legpairs of each segment; legs as described for genus, with numerous setae on ventral surfaces of first three segments; legs separated by distance of less than three coxal lengths; second legs with a pair of small, mesal, cylindrical coxal processes on posterior surface, a minute pair of swellings on anterior surface; third legs with coxal lobes larger and flatter than those of second legs, these bearing small setae and lacking lateral spine.

Gonopods with tibiotarsus narrow, curving evenly mesad beyond femoral endite, recurving slightly apically, tip acuminate; femoral branch narrow basally, widening to broad surface, rounded dorsally and ventrally, with an elongate, straight lateral process and a broader distal process curving sharply distad and narrowing abruptly to acute apex; mesal margin of femoral endite smooth.

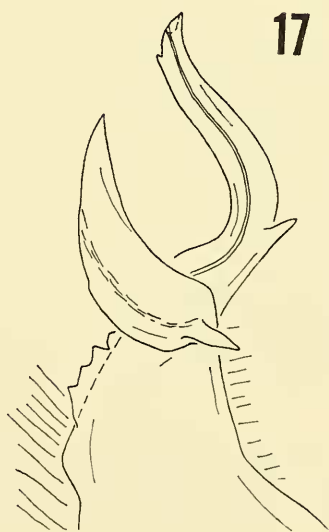
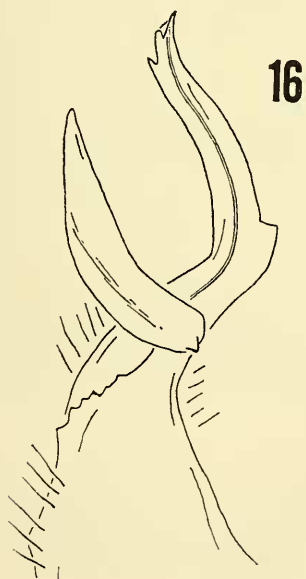
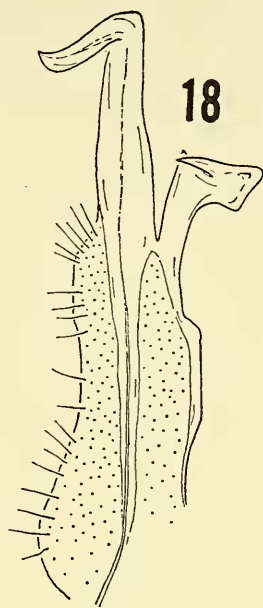
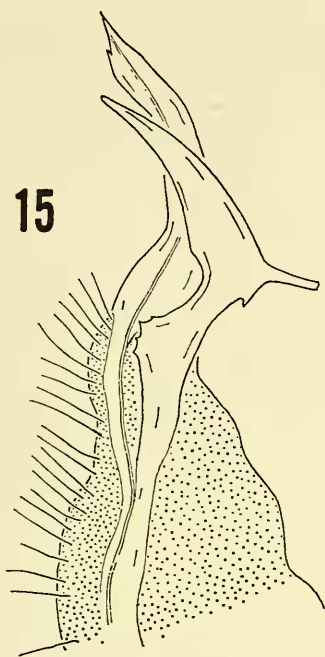
Female: As in male, but second legs with coxa thin, subtriangular, with small ventral process apically, mesad of joint with prefemur; cyphopod aperture as wide as sternal area of sixth segment, closed along posterior margin by thin sclerotized bar; socket narrowed mesally, thus longest in region of each cyphopod; anterior margin of cyphopod aperture curving evenly; cyphopods as in figure 28.

Specimens examined: Holotype male: CALIFORNIA: Placer County: 1 mile east of Auburn, 28 January 1968 (M.R., R.C., J.L., B.W. & K.B. Gardner). Paratypes: 28 males, 32 females, same data as holotype; El Dorado County: 8 males, 6 females, 1 mile north of Cool, 4 February 1968 (M.R.G.); 1 male, 3 females, 1 mile west of Greenwood, 4 February 1968 (M.R.G.); 6 males, 6 females, 2 miles west of Georgetown, 4 February 1968 (M.R.G.).

Variation: Statistics: Cool population: males, length 20–23.5mm; length/width 5.4–6.0; females, length 21.5–26mm; length/width 5.0–5.3;

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FIGS. 15–18. (Right male gonopods). 15. *W. remota*, paratype; mesal aspect. Collected 3 miles southwest of Foresthill, Placer County. 16. *W. remota*, paratype; anterior aspect. Collected from Foresthill, Placer County. 17. *W. remota*, paratype; anterior aspect. Collected 3 miles southwest of Foresthill, Placer County. 18. *W. discordis*, paratype; mesal aspect. Collected 1 mile east of Auburn, Placer County.



average population length 23.0mm. Auburn population: males, length 21.5–28mm, length/width 6.1–6.8; females, length 21.5–30mm, length/width 5.1–5.6; average population length 23.4mm. Populations east of Cool: males, length 25–28mm, length/width 6.0–6.1; females, length 28–32mm, length/width 5.2–5.7; average population length 28.2mm.

Perhaps the greatest infraspecific variability of the genus occurs in this species. Specimens from Auburn vary in degree of development of the lateral process of the femoral endite, most specimens with this process being a well developed simple or bidentate spine, although one specimen, probably a mutant, lacked the lateral process on both gonopods. The distal process of the femoral endite is always sharply curved and acutely pointed. The lateral spine of the tibiotarsus is minute on some specimens, lacking on others.

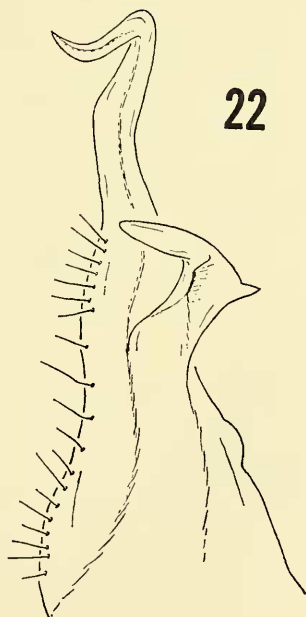
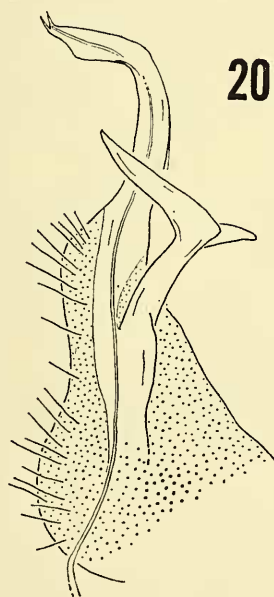
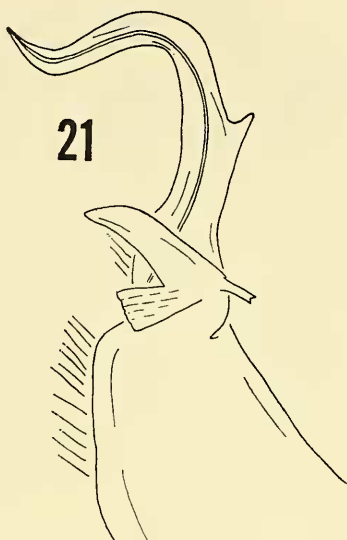
Specimens from Cool often possess a rather distinct lateral spine on the tibiotarsus, with the femoral endite exhibiting a rounded distal margin rather than notched as in the Auburn population. The distal process is sharply recurved so that it appears rounded from the anterior aspect (see fig. 11). Populations east of Cool have the distal margin of the femoral endite notched or acutely produced; the lateral process is short and bidentate to long and simple; the lateral spine of the tibiotarsus is small but distinct.

Ecology: Collected at 1,000' on the American River at Auburn and 2,200' west of Georgetown, *discordis* occupies perhaps the most diverse range of conditions found in the genus. Near the top of the northeast-facing canyon wall of the American River, the soil is red, duff is shallow, *Quercus wislizenii* and *kelloggii* low and scrubby, and *Arctostaphylos* common. At the highest elevation, near Georgetown, where the hillside remains partially covered with snow, *Pinus* spp. provide the dominant ground litter, although tall oaks and smaller herbaceous plants abound on the hill also. The ground litter is generally thick (2–8cm). Specimens were found in areas of the slope where low brush was minimal, and oak leaf litter the most prevalent. The large size of individuals at the higher elevations is possibly a reflection of the richer food source available.

Distribution: Four collections have been made in a line 12 air-miles long between Georgetown and Auburn, with one collection on the west bank of the American River eliminating the river as an effective barrier. Closely bordered by *remota* to the north and *placera* to the south, *discordis* is probably a localized form.

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FIGS. 19–22. (Right male gonopods). 19. *W. sierrae*, paratype; anterior aspect. 20. *W. sierrae*, paratype; mesal aspect. 21. *W. hoffmani*, paratype; anterior aspect. Collected 1 mile north of Shingle Springs, El Dorado County. 22. *W. hoffmani*, paratype; mesal aspect.



Wamokia hoffmani Buckett and Gardner new species
(Figures 21, 22, and 27)

Holotype: Male, 1 mile north of Shingle Springs, El Dorado County, California; deposited in Type Collection, (UCD).

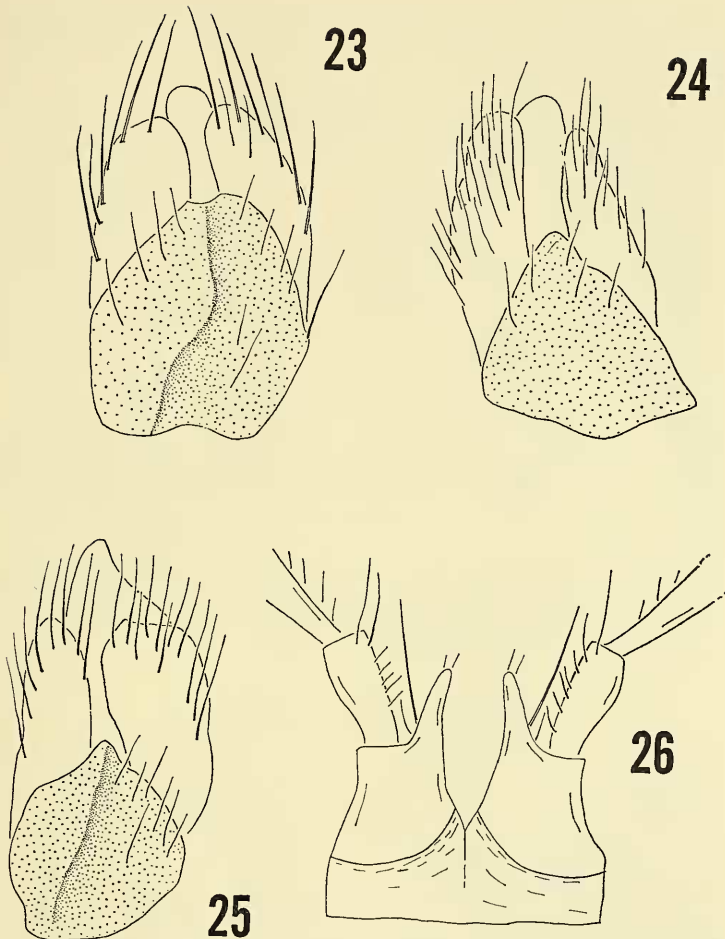
Diagnosis: Resembling *falcata* and *dentata* in the small distal process and very small lateral process of the femoral endite, but distinguished from these and other known members of the genus by the possession of two processes projecting mesad from the femoral endite. The lateral process may be present or absent.

Description: Holotype male: Color in life orange on lateral tips of collum and other segments, this color extending across posterior part of metatergite, a longitudinal medial black stripe present from collum to antepenultimate segment. Head with smooth, deep coronal suture, dividing between antennae to inconspicuous frontal sutures; vertigial area dorsad of antennae with a number of small wrinkles; 4 supra-antennal, 9 frontal, 20 clypeal and 22 labral setae present; 7 setae along lateral margin of facial shield between labrum and ventral margin of antennal groove; gular area with broad, shallow groove parallel to antennal groove. Collum typical of genus, much exceeded ventrally by second segment; tergites generally smooth with fine longitudinal striae on anterior half of metatergite, posterior half with about seven low longitudinal wrinkles on each side of segments of caudal half of body; segments 17-19 reduced in size, telson much surpassing anal valves and possessing regular 14 setae; anal valves well developed, with 2 pair of setae. Metazonites ventrally sunken at point of contact with prozonites, sterna raised out from body level mesally about one-fourth their lateral height, a shallow longitudinal groove present on sterna between anterior and posterior legs of each segment; posterior and anterior pairs of legs separated by the same distance, equal to two coxal widths.

Gonopods with lateral spine located on tibiotarsus about $1.2 \times$ distance from origin of femoral endite to its apex; tibiotarsus strongly curving mesally distad of lateral spine, the apex acuminate and slightly recurved; femoral endite short, broad, with acute distal process longest, projecting mesocaudad; basal process more directly mesad, truncate with uneven mesal margin; lateral process distinct, narrow and acute.

Female: As in male, except for secondary sexual characters; second legs with coxa flat, a distinct cylindrical process present; cyphopod aperture with posterior margin evenly rounded, a low mesal swelling present; cyphopods as in figure 27.

Specimens examined: Holotype male: CALIFORNIA: El Dorado County: 1 mile north of Shingle Springs, 20 January 1968 (J. S. Buckett & M. R. Gardner). Paratypes: 14 males, 34 females, same data as holotype; 2 males, 2 females, 2 miles north of Shingle Springs, 16 April 1965 (M.R.G.); 37 males, 19 females, 4 miles southwest of Shingle Springs, 4 February 1968 (M.R.G.); 2 males, 2 females, 6 miles south of El Dorado, 28 November 1964 (J.S.B. & M.R.G.); Amador County:



FIGS. 23-26. (Female cyphopods, mesal aspect). 23. *W. dentata*, paratype. 24. *W. placera*. Collected 2 miles north of Placerville, El Dorado County. 25. *W. remota*, paratype. Collected 3 miles southwest of Foresthill, Placer County. 26. *W. placera*, paratype female; sternum and basal segments of second legs.

2 males, 2 females, Cosumnes River, southeast of Latrobe, 26 November 1965 (M.R.G.).

Variation: Population from 4 miles southwest Shingle Springs: males length 21-24mm, length/width 5.4-5.9; females length 23-25mm, length/width 4.8-5.6; average population length 23.3mm. Population

from 1 mile north of Shingle Springs: males, length 23–26mm, length/width 5.6–6.2; females length 23–28mm, length/width 4.8–5.5; average population length 24.5mm.

Specimens from southwest of Shingle Springs differ from the holotype by possessing a longer distal than basal process on the femoral endite, and either lacking the lateral process entirely or exhibiting a small, rounded protrusion. Also in this population the lateral spine of the tibiotarsus is minute, and variable in its position. Specimens from Cosumnes River possess a distinct lateral process on the prefemoral endite and a large lateral spine, which is positioned lower on the tibiotarsus than in other populations. Individuals from south of El Dorado have the lateral process either lacking or small and spiculate; the lateral spine of the tibiotarsus is prominent and low as in individuals of the Cosumnes population.

Ecology: *W. hoffmani* has been collected at elevations of 600' to 1,400' in areas of red soil with plant cover of mixed stands of *Quercus wislizenii* and *kelloggii*, and with occasional specimens of *Pinus sabiniana*. Populations of millipeds were dense at least at the two localities near Shingle Springs, numbers averaging about 20 individuals per square yard of ground.

Distribution: This species possesses the greatest known distribution, extending longitudinally from the south bank of the Cosumnes River to 2 miles north of Shingle Springs, a distance of about 15 air-miles. Latitudinally, the distribution is 8 miles wide.

Wamokia placera Chamberlin
(Figures 3, 4, 9, 10, 24, and 26)

Wamokia placera Chamberlin, 1941. Bull. Univ. Utah, biol. ser., 6(5): 14, fig. 27.

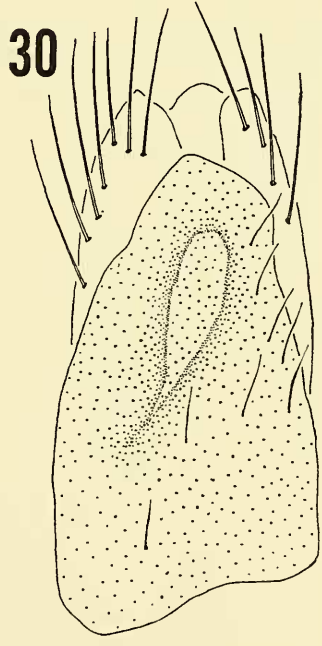
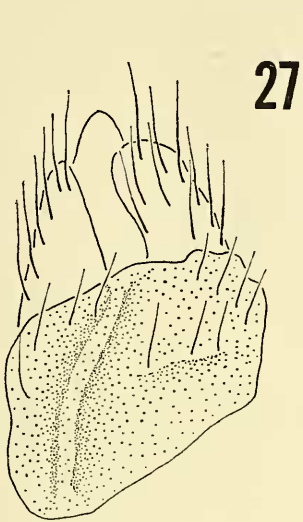
Type: Holotype: 9 miles north of Placerville, El Dorado County, California, probably in the vicinity of Coloma; presently in the collection of the late R. V. Chamberlin.

Diagnosis: Characterized by the development of the femoral endite into an almost straight, acute distal process and a broad, prominent lateral process which projects lateroproximad, and is subequal in width to distal process.

Description: Male: Head with usual coronal suture, frontal sutures weak; head smooth, but with very fine, impressed vertical lines on vertex; short horizontal lines on frons and gula; frons with irregular row of 9 setae; clypeus with row of 23 setae and labrum with 22 setae; gular region with shallow, although distinct, groove parallel to lateral

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FIGS. 27–30. (Female cyphopods, mesal aspect). 27. *W. hoffmani*, paratype. Collected 1 mile north of Shingle Springs, El Dorado County. 28. *W. discordis*, paratype. Collected 1 mile east of Auburn, Placer County. 29. *W. sierrae*, paratype. 30. *W. falcata*, paratype.



margin of facial shield; a row of 6 right and 4 left setae present along lateral margin of gula from clypeus to half the distance toward antennal groove; antennae of normal proportions, spaced by distance equal to length of third segment. Collum wider than head, anterior margin evenly curving with posterior corners back as far as posterior margin of segment. Tergites generally smooth, with short, longitudinal etchings; last four segments becoming reduced, telson with usual 14 setae, much surpassing well developed anal lips; preanal scale longer than half its width, obtusely angular caudad. Sterna raised very little mesially, half a coxal width laterally, with fine longitudinal striations and a shallow transverse groove present between legpairs of each segment. Legs long, of usual segmental proportions, on postgenital segments separated by about 2.3 coxal lengths; second legs with small pair of ventral coxal processes, third legs with broader, longer processes located relatively further laterad than those of leg 2.

Gonopods with telopodite distally narrowing to half width of femoral region; tibiotarsus curving distad and slightly mesad for two-thirds its length, then strongly curved inward and slightly proximad, the apex acuminate and curved again mesodistad, lateral spine lacking; femoral endite very narrow near base, produced strongly cephalad away from tibiotarsus, with distal process long, straight and acute, and lateral process curved proximad, short, but stout, its basal area as wide as distal process; mesal margin of endite smooth, not produced mesad, and separated from femur for much of its length.

Female: As in male, except for the following sexual characters: posterior margin of cyphopod socket curved, meeting mesad between cyphopods; second legs with coxa thin, subtriangular, with a distinct cylindrical distal process; cyphopods as in figure 26.

Specimens examined: CALIFORNIA: El Dorado County: 9 males, 8 females, 2.1 miles north of Placerville, 4 February 1968 (M. R. Gardner); 7 males, 12 females, 3 miles southwest of Placerville, 13 January 1968 (J. S. Buckett & M. R. G.).

Variation: Population southwest of Placerville: males, length 22.5–28mm, length/width 5.6–5.9; females, length 26–30mm, length/width 5.0–5.4; average population length 26.8mm. Population north of Placerville: males, length 27–29mm, length/width 5.3–5.9; females, length 26–31mm, length/width 5.2–5.5; average population length 28.5mm.

Of the two collections we have made, variability in the gonopods is insignificant, a slight difference in the curvature of the tibiotarsus being the only evident difference between the two populations.

Ecology: Collections have been made by us at elevations around 1,600'. The type collection, if from near Coloma, was made at about 800'. The localities at which we collected *placera* were on northeast facing 30° slopes, with the oaks *Q. wislizenii* and *kelloggii* dominating the composition of the ground litter, the soil being red Aiken Clay.

Distribution: We have made two collections 4 miles apart in the vicinity of Placerville. Including the type locality, 9 miles north of Placerville, the known range exceeds a little over 10 air-miles in a north-south direction, and will probably not be found to extend much further.

***Wamokia dentata* Buckett and Gardner new species**
(Figures 13, 14, and 23)

Holotype: Male, 3 miles northwest of Somerset, El Dorado County, California; deposited in Type Collection, (UCD).

Diagnosis: Similar to *falcata* in configuration of the distal and lateral processes of the femoral endite, but distinguished by the dentate mesal margin of the femoral endite and more basal location of lateral spine or telopodite.

Description: Holotype male: Color typical of genus, orangish-grey dorsally with orange on both surfaces of lateral and posterior margins of paranota. Head with coronal suture smooth, prominent, dividing between antennae to two frontal sutures which are evident only for distance between antennae and lower seta just ventromesad of antennae; frons smooth, but with shallow transverse sculptured lines; lower part of frons with transverse row of 8 setae; 5 setae in row along lateral margin of facial shield from clypeus half the distance to antennae; clypeus with transverse row of 22 setae; labrum with transverse row of 33 setae; genae smooth, with impressed groove parallel to supra-antennal groove; antennae widely separated, distance between them equal to length of second antennal segment; antennal segments as in generic description. Collum wider than head but narrower than following segments, anterior margin curving in even semicircular arc, the posterior corners even with posterior margin of segment; segments 17 and 18 progressively smaller and narrower, segment 19 much reduced, paranota projecting caudad only slightly beyond posterior corners of segment 18; telson subtriangular, broader than long, with 14 setae; anal valves smooth, much surpassed by mucro, with 2 pairs of setae lining lips; preanal scale large, sublenticular, about half as long as broad, with a pair of setae on posterior margin. Sterna smooth, raised out from level of body and curved with lateral margins much more produced than mesal area, the coxae projecting at 45° from horizontal, a transverse groove present; legs with prefemoral spine beginning on segment 9 and progressively increasing in size posteriorly, the posterior leg of each segment with greater spine development; second coxae each with large cylindrical process produced anteroventrad.

Gonopods similar to *placera*, with tibiotarsus long and narrowing evenly though rapidly from connection with femur, and bent mesad near distal margin, with apex curved again distad; lateral spine of tibiotarsus minute; femoral endite with basal region small, but distal process large, curving evenly mesodistad and narrowing evenly to acuminate apex;

mesal margin of femoral endite serrate; lateral process elongate and truncate, though small.

Female: Female with prominent setose processes on flat second coxae; cyphopod socket with posterior rim swollen mesally. Cyphopods as in figure 23.

Specimens examined: CALIFORNIA: El Dorado County: Holotype male, 3 miles northwest of Somerset, 20 January 1968 (J. S. Buckett & M. R. Gardner). Paratypes: 3 males, 15 females; same data as holotype.

Variation: Male, length 22–24mm, length/width 5.3–6.0; female, length 25–28mm, length/width 5.1–5.6. Gonopods not noticeably variable.

Ecology: The one collection of this species was made on a gently (ca. 12°) sloping hillside covered with *Q. wislizenii*, with thin surface litter. Notably, this is the only collection of *Wamokia* made in an area of black soil.

***Wamokia falcata* Buckett and Gardner new species**
(Figures 7, 8, and 30)

Holotype: Male, Camino, El Dorado County, California; deposited in Type Collection, (UCD).

Diagnosis: Distinguished from *dentata*, its closest relative, by the lack of a serrate mesal margin of the femoral endite, and by the presence of prominent lateral spine located well distad of the apex of femoral endite.

Description: Holotype male: Color faded in alcohol. Head with frontal sutures barely evident, with frontal and supra-antennal setae present; lower part of frons with transverse row of 8 setae; clypeus with 20 setae in transverse row; labrum with 23 setae in transverse row; 5 setae in row along lateral margin of facial shield from clypeus to half the distance to antennae; gena with groove very shallow, barely evident; antennae of normal configuration, separated by distance equal to length of third antennal segment, first, second and third segments with long distal setae. Collum with posterior margin convex laterally, concave mesially, with rather sharp posterior corners; tergites smooth; nineteenth segment small, exceeded by paranota of eighteenth segment; telson with 2 pairs of lateral setae, posterior pair just cephalad of posterior dorsal setae, with 2 pairs of terminal setal sockets, though setae missing; telson surpassing anal valves, which are smooth, with 2 pairs of setae lining anal lips. Sterna almost even with prozonites mesially, raised out laterally, longitudinal wrinkles present mesad of leg sockets; prozonites separated from metazonites by narrow rim ringing segment, followed by shallow groove. Legs long, extending well beyond lateral margins of segment, the relative length of segments from longest to shortest being 3, 2, 6, 5, 1, 4; both anterior and posterior coxae with row of 10–12 stout setae and 1 long seta.

Gonopods large, well exerted from socket, with tibiotarsus broad proximad of large lateral spine, the narrow distal continuation arching mesocephalad, the apex acuminate, recurved; femoral endite much shorter than tibiotarsus, arising mesocephalad from half the overall length of telopodite, projecting strongly laterad to lateral margin of tibiotarsus, then curving evenly mesodistad and narrowing gradually to acuminate apex, a small rounded lateral process present; the mesal margin of base of femoral endite much produced, entire, concealing part of tibiotarsus from cephalic aspect.

Female: Second leg with coxa flat, subtriangular, and with a prominent elongate distal process; cyphopod aperture with anterior margin essentially straight for much of its length, with small, abruptly produced mesal process. Cyphopods as in figure 30.

Specimens examined: CALIFORNIA: El Dorado County: Holotype male, Camino, 24 December 1964 (S. Seminoff). Paratypes: 1 male, 2 females, same data as holotype.

Distribution: Known only from one collection, this entity is bounded on the west by *placera*, and on the south by *dentata*. The situation to the north is not known.

***Wamokia remota* Buckett and Gardner new species**
(Figures 15, 16, 17, and 25)

Holotype: Male, 8 miles northeast of Auburn, Placer County, California; deposited in Type Collection, (UCD).

Diagnosis: Distinguished from most species in the genus by the presence of a long distal process, subequal to tibiotarsus in length and exceeding it in width; tibiotarsus not curving strongly mesad as in other species of the genus. Distinguished from *sierrae* by the presence of a prominent lateral spine and serrate mesobasal margin of femoral endite.

Description: Holotype male: Color in life bright orange on tips of collum and paranota; beige across prozonites dorsally, light brown across metatergites, telson orange.

Head with 2 pairs of supra-antennal setae, uneven transverse row of 8 frontal setae, about 20 prominent clypeal setae and 23 prominent labral setae; head smooth and shining above, sparsely transversely sculptured medially, this fine sculpturing dense on ventral third; antennae well spaced, slightly less than length of second segment apart. Dorsum of tergites smooth except for short, minute longitudinal striae; collum with anterior margin forming smooth arc, with least curvature mesad over head, posterior margin sinuous, convex laterad and concave mesad; segments 17-19 increasingly reduced, paranota of 19 small, rounded lobes barely projecting caudad beyond posterior margin of segment; telson with usual 4 dorsal, 6 lateral, 4 apical setae; anal lips moderately prominent. Sterna finely striate, on postgenital segments medially low, barely raised out from level of body, with a longitudinal and transverse groove, laterally more pronounced, lacking longitudinal wrinkles; legs

separated by distance equal to two coxal lengths, posterior legs of median body segments slightly more separated than anterior legs; pregenital legs with sterna more produced; prefemur of legs with apical spine, femur becoming very long at posterior end of body.

Gonopods with tibiotarsus broad, shorter than in other species, curving slightly mesad though much exceeded by femoral endite; tibiotarsus with apex notched, truncate, and with prominent lateral spine near base; femoral endite curving laterad, then curving strongly mesad; endite exceedingly broad, equal to twice or more breadth of tibiotarsus distad of lateral spine, near apex curving distad toward apex of tibiotarsus and evenly narrowing to sharply acute apex; lateral process of endite as large as lateral spine of tibiotarsus, located proximad and directed laterad; mesal margin of base produced, strongly dentate.

Female: Coxa of second legs with prominent cylindrical ventral processes; posterior margin of cyphopod socket of two convex arcs meeting mesad between cyphopods. Cyphopods as in figure 25.

Specimens examined: CALIFORNIA: Placer County: Holotype male, 8 miles northeast of Auburn, 28 January 1968 (M. R., R. C., J. L., B. W. & K. B. Gardner). Paratypes: 29 males, 33 females, same data as holotype; 11 males, 16 females, 3 miles southwest of Foresthill, 28 January 1968 (same collectors as preceding); 1 male, Foresthill, 24 April 1965 (J. S. Buckett).

Variation: Auburn population: males, length 22–24.5mm, length/width 5.3–6.8; females, length 22.5–28mm, length/width 5.0–5.4; average population length 24.7. Population 3 miles southeast Foresthill: males, length 21.5–24mm, length/width 5.7–6.9; females, length 24–27mm, length/width 4.9–5.8; average population length 24.0mm.

In the gonopods, variability is found in the lateral process of the femoral endite. In the single specimen from Foresthill, a slight bump lies in the place of the distinct spine-like lateral process found in other specimens. Specimens from northeast of Auburn are very similar to those southeast of Foresthill. One difference lies in the length of the lateral spine of some of the Auburn specimens greatly exceeding those of the Foresthill population and being the most strongly developed in the genus. The spine can be either simple or bidentate.

Ecology: Collections of *remota* have been made at elevations of approximately 2,000, 3,000 and 3,200', the latter two localities being above snow line much of the winter. At the localities 8 miles northeast of Auburn and 3 miles southwest of Foresthill, specimens were collected in areas of red clay soil, with *Q. wislizenii*, *Q. kelloggii* the dominant vegetation. Specimens occurred in areas of the hillside where oak ground litter was apparently deepest, with as many as 25 individuals occurring in a single square yard.

Distribution: Known from localities spanning 9 miles in latitude in Placer County just north of the Middle Fork of the American River,

which probably forms the southern boundary. The northern boundary remains unknown.

***Wamokia sierrae* Buckett and Gardner new species**
(Figures 19, 20 and 29)

Holotype: Male, 1 mile southwest of Grass Valley, Nevada County, California; deposited in Type Collection, (UCD).

Diagnosis: Distinguished from *remota* by the long tibiotarsus which curves strongly mesad, the apices overlapping in situ, with lateral spine lacking or minute, and by the untoothed mesal margin of the base of the femoral endite; distinguished from other species by the very long blade-like distal process, with prominent lateral process arising directly from base of distal process.

Description: Holotype male: Head with typical distinct coronal suture, 1 pair of supra-antennal setae on each side; vertex and frons marked by short, impressed striations, otherwise smooth; a pair of setae present on frontal suture below antennae; setae between antennae lacking; frons with uneven transverse row of 10 setae above clypeus; clypeus with 26 transverse setae, labrum with 28 setae; gena with shallow groove parallel to margin of facial shield; a row of about 10 setae on lateral margin of gena; antennae separated by distance equal to length of second antennal segment; sixth antennal segment longer than second antennal segment. Collum anteriorly curving in even posterior arc, lateral corners round, even with posterior margin of segment; paranota of mid-body segments evenly rounded antero-laterally, the posterior corners acutely produced; on posterior half of body, pore bearing segments with lateral margins of paranota swelled; segments smooth dorsally, marked only by fine longitudinal striations; segments 17-20 progressively reduced, paranota of penultimate segment projecting caudad only slightly; anal tergite subtriangular, with usual 14 setae; anal lips weakly produced, with two pairs of setae lining lips. Preanal scale suboval, with 2 apical setae. Sterna essentially flat, coriaceous, low medially but raised out laterad to half coxal width, a deep transverse groove between legpairs; legs as described for genus, distal 3.5 segments extending beyond lateral margins of paranota; legs 2 and 3 with rounded coxal processes, those of second legs much the smaller and projected caudad, those of third legs projected ventrad. Prefemoral spines prominent in postgenital segments.

Gonopods with tibiotarsus narrowing beyond femoral endite, lateral spine lacking on right gonopod, minutely represented on the left; tibiotarsus curving laterad, then evenly mesad, the apex acute, curved distad; femoral endite narrowing beyond base, then abruptly dividing into broad blade-like distal process and straight lateral process; distal process subequal to tibiotarsus mesally, but much exceeded by it distally, the lateral margin concave; lateral process straight, acute, projecting directly laterad.

Female: Cyphopod aperture with posterior margin nearly straight, but with low mesal swelling present; coxa of second legs more rounded than in other species, possessing short ventral cylindrical processes. Cyphopods as in figure 29.

Specimens examined: CALIFORNIA: Nevada County: Holotype male, 1 mile southwest of Grass Valley, 10 February 1968 (J. S. Buckett & M. R. Gardner). Paratypes: 5 males, 7 females, same data as holotype.

Variation: Males: length 21–23mm, length/width, 5.6–5.8; females: length 23–24mm; length/width 4.8–5.6. Average population length 22.9mm. The lateral spine of the tibiotarsus is the only noticeable variable gonopod character. In most specimens, the spine is absent, but on the holotype, a minute remnant is present on the left gonopod, though absent on the right gonopod.

Ecology: *W. sierrae* inhabits the most unusual econiche of the known species in the genus. At 2,500' elevation, the area is typical pine forest composed of *Pinus ponderosa* and *P. jeffreyi*, with low shrubs and occasional scrubby *Quercus wislizenii* and *kelloggii*. The collection was made beneath the largest *Q. wislizenii*, where the ground was covered with a thick mat 3–4" thick of oak leaves and pine needles fused with fungus. Most specimens were in the zone between the red soil and the litter mat, although a few occurred in the mat itself.

Distribution: With only one collection known, *sierrae* is set off by over 15 air-miles from the nearest collection of *Wamokia*. This northern area of the generic range is where future collecting should be concentrated for the possible discovery of new species.

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